

TRANSFER TO INTERMEDIATE FORMS FOLLOWING CONCEPT DISCRIMINATION BY PIGEONS: CHIMERAS AND MORPHS

NATASHA GHOSH, STEPHEN E. G. LEA, AND MALIA NOURY

UNIVERSITY OF EXETER

Two experiments examined pigeons' generalization to intermediate forms following training of concept discriminations. In Experiment 1, the training stimuli were sets of images of dogs and cats, and the transfer stimuli were head/body chimeras, which humans tend to categorize more readily in terms of the head part rather than the body part. In Experiment 2, the training stimuli were sets of images of heads of dogs and cats, and the intermediate stimuli were computer-generated morphs. In both experiments, pigeons learned the concept discrimination quickly and generalized with some decrement to novel instances of the categories. In both experiments, transfer tests were carried out with intermediate forms generated from both familiar and novel exemplars of the training sets. In Experiment 1, the pigeons' transfer performance, unlike that of human infants exposed to similar stimuli, was best predicted by the body part of the stimulus when the chimeras were formed from familiar exemplars. Spatial frequency analysis of the stimuli showed that the body parts were richer in high spatial frequencies than the head parts, so these data are consistent with the hypothesis that categorization is more dependent on local stimulus features in pigeons than in humans. There was no corresponding trend when the chimeras were formed from novel exemplars. In Experiment 2, when morphs of training stimuli were used, response rates declined smoothly as the proportion of the morph contributed by the positive stimulus fell, although results with morphs of novel stimuli were again less orderly.

Key words: concept discrimination, global features, local features, spatial frequency, generalization, key peck, pigeon

In concept discrimination tasks, animals are trained to discriminate between sets of stimuli that are defined in terms of concepts held by the human experimenter (see Lea, 1984). Where the concepts concerned correspond to natural-language categories, such as "human," it is widely accepted that they are polymorphous (Ryle, 1949); that is, there is no single necessary or sufficient condition for a stimulus to be an instance of the concept, and artificial concepts that meet this criterion have frequently been used in research (e.g., Lea & Harrison, 1978). It is therefore common practice in concept discrimination experiments to conduct transfer tests after ac-

quisition using imperfect exemplars of the concepts in order to determine which of the available properties of the stimulus are exerting effective control over the animals' discriminatory behavior. For example, after training pigeons to discriminate the letter "A" from the figure "2" in a range of typefaces, Morgan, Fitch, Holman, and Lea (1976) tested the birds with other letters and numbers and with rotated, fragmented, and handwritten examples of "A" and "2." Similarly, Aust and Huber (2002) trained pigeons in a human present-human absent discrimination and tested transfer of the discrimination to images of humans with different body parts obscured or missing, and Jitsumori and Yoshihara (1997) trained pigeons to discriminate happy and angry expressions on human faces and tested transfer to stimuli in which either the mouth or the eyes and eyebrow regions of the face were exchanged between stimuli.

As can be seen from these examples, such transfer tests often involve the deletion or annulment of particular local features that might be supporting the discrimination. However, such manipulations are most relevant to a multiple linear feature model of concept discrimination, and there are several

Some of the experimental work was conducted by Natasha Ghosh in partial fulfilment of the requirements for the PhD degree at the University of Exeter; the writing was completed while Stephen Lea was a Visiting Scholar at the University of California, Berkeley, and thanks are due to Lucy Jacobs for facilities provided there. Thanks also to Alan Slater and to Paul Quinn of Washington and Jefferson College for discussion, to Janine Spencer of Brunel University for providing some of the stimuli used, to Catriona Ryan for technical support, and to Kazuhiro Goto for his comments on the manuscript. Animal housing and the conduct of all experimental work were in accordance with the requirements of the United Kingdom Animals (Scientific Procedures) Act, 1986.

Reprints may be obtained from Stephen Lea (e-mail: s.e.g.lea@exeter.ac.uk).

known difficulties with such a model (Lea, Lohmann, & Ryan, 1993). Alternative accounts that have been suggested include absolute discrimination (e.g., Vaughan & Greene, 1984), prototype theory (e.g., Huber & Lenz, 1996), and Biederman's geon theory (Wasserman *et al.*, 1996). All of these alternative accounts imply that a more informative way of producing imperfect stimuli for transfer tests is to alter the overall appearance of the stimuli rather than interfering with local features.

Two ways of producing such an overall alteration have been used in the literature. Both are relevant to the case of discrimination between two distinct categories of stimuli rather than between the presence and the absence of a single category. The first is to construct intermediate stimuli from sections of positive and sections of negative stimuli (e.g., Cook, Wright, & Kendrick, 1990); such stimuli are called chimeras. The second is to produce a point-by-point mixture of two images; the first technique of this sort was Galton's (1883) use of composite photographs, but the modern approach is to use computer morphing. This technique recently has begun to be used in concept discrimination work with pigeons (e.g., Makino & Jitsumori, 2001).

Although both chimeras and morphs involve changing many features of the original stimuli at once, the two techniques have markedly different effects at the level of the kinds of features that may be supporting concept discrimination. Chimeras retain all the detailed, high spatial frequency information from the original stimuli (though they may combine it in unfamiliar ways) while changing the overall shape, which is carried by low spatial frequencies. Morphed images dilute all features and leave nothing entirely unchanged, but a moderate degree of morphing will have a bigger effect on the details of the stimuli (i.e., on high spatial frequencies) than on its overall shape (i.e., on low spatial frequencies). Cerella (1986) and Cavoto and Cook (2001) have suggested that pigeons tend to rely more on local cues compared with humans, which means that they should be disproportionately affected by manipulations affecting high spatial frequencies. If local feature dominance is a general tendency, it should be reflected in different patterns of

generalization to chimeras and morphs. With chimeras, local feature dominance should lead to unimpaired responding to stimuli that contain the key local features and much reduced responding to those that do not; with morphs, it should lead to sharp generalization decrement to any morphed stimulus. If global features are important, however, all chimeras should lead to marked generalization decrement (because they all produce a wholly new overall shape), though some may lead to less reduction in responding if they include parts of the stimuli that are particularly influential on its overall shape. Because morphing only changes global shape gradually, a more graduated response to this manipulation might be expected.

The aim of the present experiments, therefore, was to compare generalized responding to these two different kinds of intermediate forms, starting from similar training stimuli and procedures. The experiments used images of cats and dogs: whole animals in Experiment 1 and heads only in Experiment 2. These are not natural categories in the biological sense, because extant breeds of dogs and cats are the result of processes of artificial rather than natural selection. However, nothing in any current theory of category discrimination restricts it to biologically derived categories. Equally, nothing in the analysis that follows depends on the assumption that the pigeons recognized the images as depictions of natural objects (i.e., cats and dogs) and, given the limited experience of the pigeons used, the probability is that they did not. The image categories were used because they were conveniently available instances of natural language categories that are, as is typical for such categories, polymorphous.

EXPERIMENT 1

The first experiment tested transfer to chimeras. The stimuli used were images of cats and dogs, chosen because these categories had been used by Quinn, Eimas, and Rosenkrantz (1993) and Quinn and Eimas (1996) in experiments on concept discrimination in infants, hence data on humans' ratings of the typicality of the individual stimuli were available. They have also been used by Mareschal, French, and Quinn (2000) in a connectionist simulation of infants' performance, and with

pigeons in previous experiments by Ghosh (2002, chap. 5 and 6). The chimeras were formed in the same general way as those used by Cook et al. (1990); that is, the training images showed whole animals in profile view, and the chimeras were formed from the head region of one animal and the body region of another.

Head/body chimeras are interesting for two reasons. The first is in relation to comparison between species. Using a procedure in which generalization was assessed by the dishabituation of the infants' characteristic response of looking selectively at novel stimuli, Spencer, Quinn, Johnson, and Karmiloff-Smith (1997) tested infants with dog/cat chimeras following exposure to whole dogs and whole cats. They found that the results depended on the length of time during which infants were able to view the original stimuli. Following brief habituation, response to the chimera depended wholly on the nature of its head: The looking response returned to its previous strength if and only if the head of the chimera was novel. Following longer viewing, dishabituation was observed with novel body cues as well as novel head cues. Preferential responding to head cues was also found with silhouettes of the stimuli by Quinn, Eimas, and Tarr (2001). There are two possible interpretations of this result: it could derive from objective properties of the parts of the stimuli—there might simply be more information present in the head part—or it could derive from a preference for looking at faces, which is evident in human infants from a very young age (e.g., Valenza, Simion, Cassia, & Umiltà, 1996). In the former case, pigeons would be expected to share the human tendency to categorize chimeras in terms of their heads; in the latter case, they might not.

Secondly, responding to head/body chimeras is relevant to the suggestion that pigeons are more influenced than humans are by the local details of a stimulus. A head/body chimera is not a simple 50% mixture of two stimuli. On the one hand, the head region is smaller, but the presumption from humans' preferential use of head information is that it contains most of the detailed information present. On the other hand, the head contributes little to overall shape, which comes from the body. Thus a head/body chi-

mera should take its overall or global shape from the body constituent, but much of the local detail that is relevant to species identification from the head constituent.

An apparent disadvantage of a head/body chimera is that the two parts are not equal in area. This, however, is inevitable if they are to contain broadly similar amounts of visual information, given that the head part contains more detailed information than the body part. Using head/body chimeras does not produce a perfect segregation of global and local features in the way that can be done by using hierarchical stimuli (e.g., Cavoto & Cook, 2001). In terms of the cues used by humans, however, there is a clear dominance of local features in the head region and of global features in the body region. This dominance is sufficient to support the prediction that pigeons' response to chimeras should be predominantly based on head cues if the cues used by humans are an unbiased sample of those available in the stimulus and if the pigeon's tendency to precedence of local information is general.

Experiment 1 therefore set out to test: (a) Whether dominance by head cues, similar to that shown by human infants, is found in pigeons. To test for such dominance, the experiment included a comparison of chimeras formed from cat heads and dog bodies with those formed from dog heads and cat bodies; and (b) whether discrimination in pigeons showed a reliance on a wider range of cues following more exposure, as reported by Spencer et al. (1997) in human infants. In the present experiment, a generalization test was conducted when the pigeons first showed evidence of discrimination and was compared with generalization after performance had reached asymptotic levels. In addition, a test of generalization to novel whole cat and dog images was included to ensure that the pigeons' behavior had come under the control of general properties of the stimulus sets rather than individual images.

METHOD

Subjects

Ten experimentally naive pigeons were drawn from a flock maintained in the laboratory's rooftop aviary. During the experiment they were housed in an indoor aviary,

measuring 2.2 m by 3.4 m by 2.4 m. The indoor aviary was equipped with pigeonholes in units of 16, and ad-lib access to water and crushed oyster shells was available. The pigeons were maintained on a 12:12 hr light/dark cycle, with 30 min simulated dawn and dusk periods. They were moved from the indoor aviary to individual cages for at least 30 min before and after the test sessions. Each pigeon was maintained at or over 85% of its free-feeding weight throughout the experiment by the delivery of hempseed during the experimental sessions and by supplements of mixed grain on nontesting days. Supplemental feeding on testing days was not necessary. A health supplement ("conditioner") was added to the hempseed used as a reinforcer.

Apparatus

Two identical three-key operant chambers, 690 mm by 490 mm by 390 mm, were used. Each consisted of a plywood box with a three-key intelligence panel (Campden Instruments Ltd, London), 335 mm by 350 mm, mounted centrally into the front wall. The three keys had a diameter of 25 mm and were centered 105 mm apart and 240 mm above the grid floor of the chamber. All three keys operated reed switches when struck with a force of 0.035 N. The two side keys were translucent and could be transilluminated by amber lamps. The center key was transparent, and a shutter operated by a rotary solenoid was situated behind it so that viewing a 15-in. (380 mm) monitor (CM1414E, Opus Technology® PLC), visible 150 mm behind the center key, was prevented during the intertrial intervals. This monitor was controlled by a PC-compatible computer (Pentium® 133MHz), running a stimulus selection and display program written in Borland® Delphi™. An aperture in the intelligence panel, 70 mm by 75 mm, was positioned 150 mm below the center key, giving access to a solenoid-operated food hopper attached outside of the box containing a 1:2 mixture of hemp and conditioner. A 1.0-W white light within the hopper tray signaled the availability of this food. General illumination was given by a 3.5-W yellow-lensed houselight situated 120 mm above the center key. Masking noise was generated by a ventilation fan and also provided by white noise relayed via a 35-ohm

loudspeaker mounted on the back of the intelligence panel.

A separate computer was used to generate the experimental stimuli for each test chamber. Both chambers and their stimulus generation computers were housed in a darkened testing room. A further PC-compatible microcomputer (Viglen® 4DX266) was located outside this room and controlled and recorded all experimental events and responses using a program written in Borland® Delphi™; a network link enabled this computer to instruct the computers attached to experimental boxes in the testing room to generate the stimuli. The pigeon's behavior during experimental sessions could be regularly monitored via CCD cameras fitted with a wide-angle lens, mounted outside a window in the chamber wall. Each pigeon was assigned to a single test chamber in all stages of the experiment.

Stimulus Materials

All images were natural photographs showing full color and texture scanned from hobbyists' handbooks illustrating different breeds of dogs and cats. Backgrounds were removed, and the images were presented on plain black backgrounds. Training stimuli were ten images of whole cats and ten images of whole dogs, and a further ten cat and ten dog images were used during generalization tests. The sizes of the pictures were initially adjusted so that all of them were 400 pixels along the longer dimension, equivalent to approximately 50° of visual angle from the pigeons' viewing position when pecking. Small size adjustments were made if necessary to facilitate the process of making chimeras. Each dog image was matched with a single cat image for subsequent joining. Pairs of images to be joined were chosen on the basis of their similarity in color, shape, and size; in addition, the pictures were rotated or reflected so that both members of each pair faced in the same direction at the same angle.

Chimeras were formed by deleting the head and neck region of the body from one picture and the tail and remainder of the body from the other, aligning the two half images, and using a cloning tool to match the colors in the adjoining area and a blur tool to soften any sharp edges. The image processing software used was Adobe® Photo-



Fig. 1. Experiment 1: Stimuli. Examples of images of (from top to bottom) a whole dog, a dog head/cat body chimera, a cat head/dog body chimera, and a whole cat. In the experiment, the images were shown in full color.

shop® 6. The test sessions used both the 20 chimeras that could be formed from the 10 pairs of images used during training, and the 20 that could be formed from the 10 pairs of images that the pigeons had not seen before. Figure 1 shows black-and-white renderings of examples of all the kinds of stimuli used; full color versions can be found in Ghosh (2002, Figure 31).

Procedure

The pigeons were trained by conventional means to find and eat the hemp and conditioner mixture when the food hopper was operated. They were then trained, using 3-s hopper access as the reinforcer, to make a single peck on the center key when the shutter opened to reveal the monitor with a gray uniform screen. The center-key schedule of re-

inforcement was raised over trials to a fixed interval (FI) of 12 s. The shutter closed on delivery of food reinforcement and remained closed during a 10-s timeout that followed. After successful training on this task, an observing-key procedure was introduced. At the end of the intertrial interval, the right key was transilluminated with amber light, and pecks on this key were reinforced by shutter-opening on an FI 2-s schedule; the FI 12-s schedule of food reinforcement was then made available.

Once pretraining was complete, the pigeons were trained on a successive discrimination schedule. Each trial was initiated by the observing-key schedule used in pretraining. The shutter was then opened to reveal a stimulus, which was exposed for a period that varied randomly between 10 and 16 s. At the end of this period, on positive trials, the shutter remained open until the next peck to the center key, which led to a 3-s hopper operation; on negative trials, the shutter closed immediately. Center-key pecks during the first 10 s of stimulus exposure were counted and used to assess discrimination. Trials were separated by a 5-s interval during which the keys were dark and the shutter was closed. Each session consisted of 80 trials made up of four cycles through the 20 training stimuli. Positive and negative trials were given in a pseudorandom sequence, generated afresh for each session, constrained so that no more than three negative or three positive stimuli were presented consecutively.

Sessions were given once per day, normally 5 or 6 days per week. All pigeons were trained with dog images as the positive stimuli. For each pigeon, training sessions were continued until the ρ discrimination index of Herrnstein, Loveland, and Cable (1976) exceeded .65 in a single session; a single generalization-test session was then given. Training was then continued until the ρ index reached .8 on three consecutive sessions for that pigeon, and further generalization tests were given. Following each of these later generalization tests, additional training sessions were given until the pigeon recovered the .8 value of ρ .

The test stimuli used in the generalization tests were as follows: (a) Test 1a (after reaching a ρ of .65): chimeras formed from familiar cat and dog images; (b) Test 1b (after

Table 1

Experiment 1: Results for individual pigeons in Generalization Tests 1a and 1b involving chimeras made up from parts of familiar stimuli.

Pigeon	Criterion of $\rho = .65$ (in one session)					Criterion of $\rho = .80$ (in three consecutive sessions)				
	Mean responses in a 10-s test					Mean responses in a 10-s test				
	Sessions to criterion	Whole dog	Dog head on cat body	Cat head on dog body	Whole cat	Sessions to criterion	Whole dog	Dog head on cat body	Cat head on dog body	Whole cat
Pl	2	21.84	14.25	20.25	16.50	7	29.33	17.56	28.11	19.06
Po	2	20.57	16.13	18.38	14.74	5	25.26	8.90	24.19	6.12
Am	4	26.19	24.63	30.50	16.16	7	24.65	8.00	21.22	5.88
Sh	3	15.04	13.63	14.50	11.49	8	19.00	12.50	17.50	8.00
Rd	1	24.61	20.50	22.88	17.75	7	27.55	24.00	23.00	15.00
Mn	1	19.20	16.75	18.13	17.22	10	23.11	10.23	20.22	9.55
Cx	1	12.89	11.38	11.50	8.66	8	24.85	10.25	23.50	7.55
Mk	6	29.28	26.50	27.38	25.35	8	22.76	7.13	21.25	9.99
Ax	4	22.89	21.88	22.25	21.34	13	25.56	12.88	24.63	12.28

reaching a ρ of .80): as Test 1a; (c) Test 2: chimeras formed from unfamiliar cat and dog images; and (d) Test 3: intact unfamiliar cat and dog images.

Generalization-test sessions always started with a cycle of 20 training stimuli. In the rest of the session, test images were used in every third trial so that 20 test trials were given. In Test 1a, each test stimulus was used once so the test could be completed in a single session. Half the test stimuli from each set (cat-head and dog-head) were used with positive and half with negative contingencies in force. In Tests 1b and 2, each of the 20 test stimuli was used once with positive and once with negative contingencies in force. Therefore, there were 40 test trials, and each test consisted of two sessions. In Test 3, the test images were used with appropriate reinforcement contingencies (all dog trials were positive and all cat trials were negative), but again there were two trials with each stimulus in order to maintain balance with the other tests. In all test sessions, the test stimuli were presented in pseudorandom sequence without replacement.

RESULTS

Acquisition

One pigeon failed to reach the discrimination criterion and showed no signs of improvement after 15 sessions; training of this pigeon was therefore abandoned. The re-

maining pigeons required between one and six sessions to reach the first criterion of a single session with ρ at .65 or above, and from 5 to 13 sessions (including those required to reach the first criterion) to reach the criterion of three successive sessions with ρ at .80 or above; data for individual pigeons are shown in Table 1.

Generalization Tests

Generalization Tests 1b and 2 each involved two sessions, but data from the two sessions were combined for analysis because there was no sign of any consistent differences in behavior between them. In most cases, a single session sufficed to bring performance back to a ρ of .80 after each test session.

Table 1 shows the results of Tests 1a and 1b when chimeras made up from the training stimuli were used. These data are summarized in Figure 2. Early in training (Test 1a), the most striking feature of the pigeons' response to chimeras was that stimuli with dog bodies were responded to considerably more than corresponding stimuli with cat bodies: all 9 pigeons responded more to whole dogs than to dog head/cat body chimeras, and responded more to cat head/dog body chimeras than to whole cats. There was a weaker and less consistent tendency for the pigeons to respond more to stimuli with dog heads (regardless of body type) than to correspond-

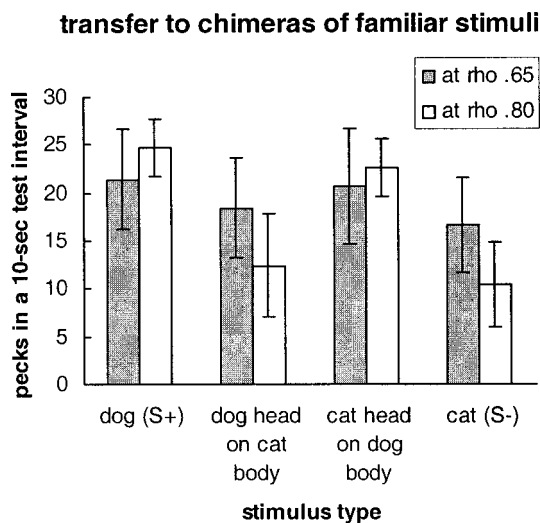


Fig. 2. Experiment 1: Results of Generalization Tests 1a and 1b. Solid bars show mean response rates of 9 pigeons to different categories of stimuli during the 10-s nonreinforced period of test trials in Test 1a (given early in acquisition). Open bars show corresponding data from Test 1b, given after reaching a more usual criterion of discrimination. The chimeras used in both tests involved were created from familiar instances of the training categories. Error bars show standard deviations across pigeons.

ing stimuli with cat heads. All 9 pigeons responded more to cat head/dog body chimeras than to dog head/cat body chimeras. When the more demanding discrimination criterion had been reached (Test 1b), the same pattern was shown but with bigger differences between the response rates to the different types of stimuli. In the mean response rates at least, the tendency to respond more to stimuli with dog heads than to corresponding stimuli with cat heads was clearer than in Test 1a, although Table 1 shows that there were still some individual exceptions to the pattern.

The statistical significance of the differences between response rates found in Tests 1a and 1b was assessed using a repeated measures analysis of variance (ANOVA). Overall analysis used three factors: the level of training at which testing was done, the species of the head of the stimulus (dog or cat), and the species of the body. The analysis revealed significant main effects of the species of head used ($F_{1,8} = 12.67, p < .01$) and the species of body used ($F_{1,8} = 105.44, p < .001$). In both cases, stimuli containing dog parts con-

trolled a higher response rate than stimuli containing corresponding cat parts. The interaction between the body species and the level of training, in which the effect on response rate of having a dog body rather than a cat body increased with more training, was also significant ($F_{1,8} = 40.34, p < .001$). No other effect approached significance.

A supplementary analysis that included only the response rates to chimeric stimuli was carried out to test the difference of effects between the two cues. There were two factors, training level and chimera type (dog head/cat body vs. cat head/dog body). The main effects of chimera type and its interaction with training level were significant ($F_{1,8}$ values of 42.90, $p < .001$ and 18.62, $p < .01$), but the effect of training level was not.

Table 2 shows individual data from Tests 2 and 3, which involved chimeras made up from novel stimuli from the training categories and novel intact instances of the training categories, respectively. The data are summarized in Figure 3, and the significance of the differences of means was assessed by a repeated measures ANOVA using stimulus category as the single factor. The differences between stimulus types were significant overall ($F_{5,40} = 24.24, p < .001$).

Supplementary analyses explored these differences further. Decrement in performance on generalization to new exemplars was assessed by an analysis that included only the intact (nonchimeric) stimuli and used two factors, old-new and dog-cat. The main effect of stimulus species was significant ($F_{1,8} = 152.33, p < .01$), and so was its interaction with the old versus new factor ($F_{1,8} = 5.85, p < .05$). A planned comparison based on the overall analysis confirmed that the significant discrimination was maintained: The difference in response rates between novel dog and cat images was significant ($F_{1,8} = 23.50, p < .01$). Table 2 shows that all 9 pigeons responded more to novel whole dogs than to novel whole cats.

Discrimination among the novel stimuli was assessed by an analysis in which the familiar stimuli were excluded and two factors were used: head species and body species (both could take two values, cat or dog). This analysis showed main effects of both head species and body species ($F_{1,8}$ values of 17.80, $p < .01$, and 23.41, $p < .001$), and also of

Table 2

Experiment 1: Results for individual pigeons in Generalization Tests 2 and 3 involving novel stimuli.

Pigeon	Mean responses in 10-s tests to stimuli containing							
	Familiar whole dog		Novel whole dog	Dog head on cat body	Cat head on dog body	Novel whole cat	Familiar whole cat	
	Test							
	2	3	3	2	2	3	2	3
Pl	26.65	28.88	28.14	28.25	27.88	21.42	18.31	17.62
Po	27.59	26.27	24.00	19.13	27.13	18.82	5.89	8.66
Am	25.31	28.08	25.83	17.13	17.88	11.92	5.63	11.53
Sh	20.00	18.59	15.59	15.00	15.50	11.67	7.93	9.28
Rd	27.58	15.50	24.42	24.38	26.75	7.25	15.69	6.11
Mn	23.34	23.62	20.59	21.00	20.50	14.67	9.20	8.93
Cx	22.62	23.93	17.36	18.75	18.50	9.10	7.30	12.14
Mk	28.50	26.04	23.90	31.75	30.63	14.80	20.58	14.16
Ax	25.47	24.03	18.67	22.63	20.75	14.80	9.55	10.88

their interaction ($F_{1,8} = 10.61$, $p < .05$). Planned comparisons based on the overall analysis showed that response rates to dog head/cat body and cat head/dog body chimeras did not differ significantly, and examination of Table 2 shows that there was no consistent trend across individual pigeons.

Response rates to dog head/cat body chimeras also differed significantly from those to novel whole cats ($F_{1,8} = 18.59$, $p < .01$), but their difference from rates to novel whole dogs was negligible.

A separate within-subjects ANOVA was used to compare the behavior towards chimeras in Test 1b and Test 2. The interaction between stimulus type and test was significant ($F_{1,8} = 23.32$, $p < .01$), confirming that behavior towards chimeras of novel stimuli was controlled in a significantly different way from behavior towards chimeras of the familiar training stimuli.

DISCUSSION

With only one exception, the pigeons learned the category discrimination between images of dogs and images of cats relatively quickly. Despite some generalization decrement, all the pigeons that learned the original discrimination showed clear generalization to new instances of the training categories (Test 3, Figure 3). We can conclude that these sets of images formed perceptually coherent categories for the pigeons, although there is, of course, no evidence as to whether they were able to relate them to real dogs or cats. Given the preexperimental history of these pigeons, it seems unlikely that they did; although they had some experience of free flight, it was in an environment in which neither dogs nor cats were com-

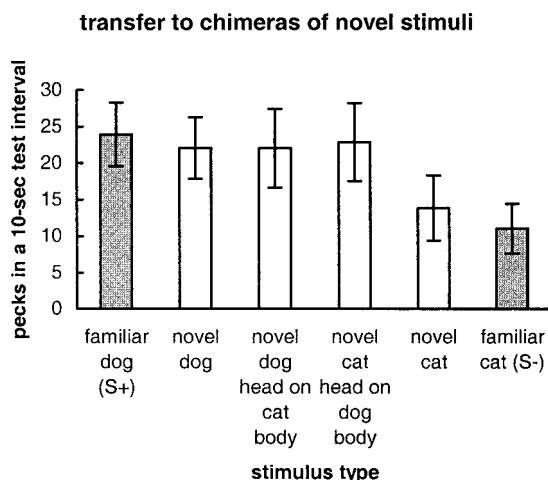


Fig. 3. Experiment 1: Results of Generalization Tests 2 and 3. The bars show mean response rates of 9 pigeons to different categories of stimuli during the 10-s nonreinforced period of test trials. Test trials involving chimeras created from novel instances of the training categories were carried out in Test 2, and test trials involving novel intact stimuli were carried out in Test 3. Error bars show standard deviations across pigeons. Data for training stimuli were drawn from Test 3, but corresponding data for Test 2 were highly similar (see Table 2).

monly seen. In any case, it is not obvious that even pigeons that do see dogs or cats frequently would need to discriminate between them.

The results of tests with chimeras formed from familiar cat and dog images differed sharply from those of human infants studied by Quinn and his colleagues (e.g., Spencer et al., 1997) in a direction that would not be expected from the hypotheses that pigeons' discrimination is relatively strongly dependent on local cues, and that local cues are concentrated in the head region. The pigeons' performance was not dominated by cues from the head area, where the high spatial frequency, local cues used by humans are concentrated. On the contrary, although both types of cue had some impact on performance, the body cues consistently had the stronger effect. Nor was there a broadening of stimulus control as training progressed: Figure 2 shows that the response rate to the dog head/cat body chimera fell with increased training, implying that the dominance of body cues over head cues was increasing. Table 2 shows that these trends in the mean results shown in Figure 2 are also typical of individual pigeons' performance. Of course, the procedures used with the two species were inevitably different, and further work is needed to ensure that the difference in results did not result from biases inherent either in the present generalization test procedure (for example, pigeons' tendency to peck rather than withhold pecking to stimuli that generally resemble those seen in training) or in the dishabituation procedure used with human infants. However, the reasonable conclusion at this point is that dominance by face cues is not greater in pigeons than in human infants.

Results of tests with chimeras formed from novel cat and dog images were significantly different from those of tests with chimeras of familiar stimuli. With novel-image chimeras, response rates for all the transfer stimuli were much closer to those for the positive stimuli than the negative stimuli, and there were no significant differences between the response rates to the cat head/dog body and the dog head/cat body chimeras, or between the rates to training dog stimuli and either kind of chimera. However, it should be noted that Test 3 showed some generalization decrement

when novel intact cats and dogs were used. Therefore, given the relatively weak control by head cues shown in Test 1, it might be argued that these cues had no detectable effect at all in Test 2, so that dog body/cat head chimeras were essentially treated in the same way as novel dogs, and the fact that they included some cat features was irrelevant. However, this argument cannot explain the fact that the novel dog head/cat body chimeras attracted much higher response rates than the novel intact cats in Test 3 (see Figure 3; this result was true of all 9 individual pigeons, see Table 2). This result makes it clear that cues from the head area did in fact have influence in Test 2.

The most economical summary of the results is that the pigeons showed good absolute discrimination of information present in the body parts of the training stimuli, and when these cues were available (as they were in Tests 1a and 1b), they dominated transfer performance. When there was no exact match to any major part of the training stimuli, the pigeons relied on more general features of the stimulus sets including information found in both the head and the body region. An influence of memory for the exact stimuli used in training, where it is applicable, is not surprising because pigeons are capable of excellent absolute discrimination of visual patterns (Vaughan & Greene, 1984). However, in the light of the ideas of Cavoto and Cook (2001), it is surprising to find that absolute discrimination is supported by the body parts of the chimeras, which to the human eye determine the global appearance of the stimuli rather than its local detail.

However, this is a human assessment, and it may be influenced by the same dominance of head cues that is found in experiments like those of Spencer et al. (1997). One way of assessing the available cues more objectively is a formal spatial frequency analysis (Campbell & Robson, 1968). The global shape of an object is determined by low spatial frequencies, whereas fine details are reflected in high spatial frequencies. If there is objectively more detailed information available in the head area of the stimuli, then we should expect a higher spatial frequency content in that area. To test this expectation, the 20 training stimuli were each divided in half, one containing the head and one the tail re-

gion. These corresponded approximately to the head and body regions used for creating the chimeras, while giving images of equal size, which was important for avoiding artifacts in the subsequent analyses. The half-images were submitted to spatial frequency analysis; the intensity profiles for each of the three color components of the digital image along a diameter of the stimulus were Fourier-transformed at each of 360 one-degree intervals, and the power spectra obtained were averaged and plotted in terms of energy per octave (as in Field, 1987). The results were unambiguous: with very few exceptions, the half-image containing the head was found to be richer in low spatial frequencies and poorer in high spatial frequencies than the half-image containing the tail (and, therefore, the main part of the body). In the light of this analysis, it seems that the pigeons' response to body cues rather than head cues in the chimeras is consistent with the evidence that, relative to humans, their behavior more readily comes under the control of local details of a stimulus rather than global properties. The breakdown of the pattern of preferential control by body parts with chimeras of novel stimuli is also explicable: with novel stimuli, detailed (high spatial frequency) information from the training stimuli is absent.

The data shown in Figure 3 are consistent with a conclusion that Quinn *et al.* (1993) reached to explain the data they obtained from human infants. Quinn *et al.* argued that the dog category is broader and more various than the cat category, and therefore infants respond to intermediate forms lacking familiar cat features as if they were dogs rather than cats. However, to be sure that the same effect is found in pigeons it would be necessary to repeat the experiment with a group of pigeons for which cat images were positive; the current data could be described equally well by saying either that images that were difficult to categorize were treated as dogs, or that they were treated as positive.

EXPERIMENT 2

The second experiment explored a different way of forming intermediate stimuli between two training categories, namely morphing. In this technique, a number of key corresponding points are identified in the

two original stimuli: for example, one point might be the tip of the left ear. The location, hue, brightness, and saturation of those points in the morphed image are calculated as a proportionate mixture of those in the two originals. All other points are then identified by reference to these key points, and hue, brightness, and saturation to be used in the morphed images are again set as mixtures of those in the originals.

The effect of morphing is to produce an image that, to the human eye, looks generally like each of the originals, but does not have any of the detailed content of either, or at least not in an unmodified form. Therefore, in the light of the discussion of the results of Experiment 1, we would expect all morphed images to be treated as true intermediates between the training categories. No part of the morphed image should match the training images exactly, so absolute discrimination of particular features of the training stimuli should play a much-diminished part in generalization.

We wanted to explore a range of different levels of morphing of dog and cat images, but we also wanted to avoid problems with subjects learning how to respond to morphed images during an extensive series of generalization tests. We therefore used a between-subjects design in which different groups of animals experienced morphs of different composition. During the generalization tests, all pigeons experienced morphed stimuli that contained a higher proportion of the dog image ("mostly dog" images), stimuli that contained dog and cat images in equal proportion ("half dog") and stimuli that contained a higher proportion of the cat image ("mostly cat"). However, the proportion of dog in the mostly dog and mostly cat stimuli varied between groups, taking values of 90%, 80%, and 60%.

In order to avoid confounding the design with the differences in processing of head and body cues that were seen in Experiment 1, the images used in Experiment 2 were of cat and dog heads only. In these stimuli, detailed information is distributed quite widely over the entire image. Also, head stimuli were more satisfactory for morphing than whole body stimuli because it was easier to identify corresponding points that led to smoothly morphed intermediate stimuli.

METHOD

Subjects

Seventeen experimentally naive pigeons were drawn from the flock maintained in the laboratory's aviary. They were divided into three groups, one of 5 and two of 6, which were exposed to the same training conditions but different generalization tests. They are referred to as Groups 60:40, 80:20, and 90:10.

Apparatus

The same apparatus was used as in Experiment 1, with the addition of two further, similar test chambers. All were arranged in the same way as those used in Experiment 1.

Stimulus Materials

All stimuli were derived from 20 pictures of dog faces and 20 pictures of cat faces. All faces were in full-face or near full-face view. Ten dog and ten cat faces were used, unmodified, in acquisition; the other ten unmodified stimuli of each type were used only in generalization tests. Additional stimuli were derived by morphing between pairs of these 40 stimuli. As in Experiment 1, the sizes of the unmorphed pictures were adjusted so that all of them were 400 pixels along the longer dimension. Each of the 20 dog faces was associated with a single cat face that was similar in color and overall shape, and the paired faces were rotated as necessary so that they faced in the same direction at the same angle. The 20 dog/cat pairs were then used to produce morphed images with the MorphMan® 2000 program (Stoik® Software); between 400 and 600 markers were placed on the two images to identify corresponding points. Figure 4 shows examples of the original and morphed images used. All stimuli were presented in full color against a black background.

Procedure

The training procedure and acquisition schedule were the same as in Experiment 1, but generalization tests were carried out only after the pigeons had reached the criterion of full acquisition (three successive sessions with a p value above .80). During acquisition, the pigeons were exposed to only 10 of the dog and 10 of the cat stimuli, the same 10 for all pigeons. Dog face images were positive for



Fig. 4. Experiment 2: Examples of the stimuli used. Top and bottom stimuli are one of the dog face images used in training and the corresponding cat; the remaining rows show morphs containing mostly dog information (90%, 80%, and 60% dog morphs), half dog information (50%), and mostly cat information (40%, 20%, and 10% dog morphs). All pigeons saw morphs with five levels of dog content, as represented by the five rows in the figure: The variations within the second and fourth rows were seen by different groups of pigeons. In the experiment, the images were shown in full color against black backgrounds.

all pigeons. Two generalization tests were given. In the first, morphed images derived from the training stimuli were used; in the second, morphed images derived from the novel images were used, and unmorphed novel images were also included. For Group 60:40, the test stimuli used were morphs composed of 60%, 50%, and 40% of the dog images; for Group 80:20, the test stimuli were morphs composed of 80%, 50%, and 20% of the dog images; and for Group 90:10, the test stimuli were morphs composed of 90%, 50%, and 10% of the dog images. Like Tests 1b and 2 of Experiment 1, each test condition con-

Table 3

Experiment 2: Results for individual pigeons in acquisition and Generalization Test 1 (morphs of stimuli used in training).

Pigeon	Sessions to criterion	Mean responses in 10-s tests to stimuli containing				
		All dog	Mostly dog	Half dog	Mostly cat	All cat
Group 60:40						
Cf	8	25.54	17.33	24.17	20.83	15.39
Ed	10	25.85	16.17	26.00	22.83	21.62
Ec	14	38.46	35.33	39.00	36.33	22.98
Sm	5	30.17	12.50	20.00	10.83	8.09
Sn	11	29.23	20.33	20.71	27.29	16.27
Group 80:20						
Ka	6	32.89	23.67	10.92	6.33	11.51
Ro	7	25.95	22.67	10.33	14.67	5.38
Ms	9	23.60	13.83	16.50	9.17	13.32
En	13	8.66	7.67	4.67	2.00	2.33
Da	19	19.09	21.17	16.83	14.17	16.38
Cu	6	33.54	34.83	23.00	25.67	18.03
Group 90:10						
Lo	7	31.54	30.83	15.67	18.50	10.28
Va	12	27.72	21.00	24.67	22.00	12.93
Cs	6	32.47	29.83	20.67	1.83	5.56
Dn	7	14.64	10.17	9.33	5.00	3.17
Pe	6	24.50	21.83	24.67	15.00	14.30
Zo	9	37.71	30.33	33.50	6.67	12.36

sisted of two sessions in order to accommodate all the test stimuli that were to be used (three morphing levels factorially combined with 10 pairs of stimuli). Test stimuli were interspersed among training stimuli, and test sessions among training sessions, according to the same rules used in Experiment 1.

RESULTS

Acquisition

All pigeons reached the criterion of three consecutive sessions with a p value exceeding .8. The numbers of sessions required for each pigeon are shown in Table 3; they ranged from 5 to 14 in Group 60:40, from 6 to 19 in Group 80:20, and from 6 to 12 in Group 90:10.

Generalization Tests

Tables 3 and 4 show individual generalization data from Tests 1 and 2, respectively. Figure 5a summarizes performance across all groups for the five categories of stimuli used in Test 1, in which morphs of the training stimuli were used, and Figure 5b gives a summary of the generalization to the mostly dog and mostly cat stimuli in this test, broken

down by group. Figures 6a and 6b show corresponding data from Test 2, in which morphs of the unfamiliar stimuli were used together with some of the intact unfamiliar stimuli.

For Test 1, using morphs of familiar stimuli, Table 3 shows that the most common pattern was for response rates to all three morphs to be between those for all dog and all cat stimuli; whereas discrimination between the all dog and mostly dog stimuli, and between the all cat and mostly cat stimuli, was most apparent in the 60:40 group and least apparent in the 90:10 group. The significance of the mean differences, as shown in Figures 5 and 6, was assessed by mixed-mode ANOVA, in which stimulus type was used as a within-subject variable and group as a between-subject variable. Stimulus type was coded as all dog, mostly dog, half dog, mostly cat, and all cat, so that the same factor levels could be used for all three groups. Separate analyses were carried through for the two test conditions; in the analysis of the data from Test 2, two "all dog" and "all cat" levels were used, one for the familiar and the other for the unfamiliar stimuli.

Table 4

Experiment 2: Results for individual pigeons in Generalization Test 2 (morphs of novel stimuli).

Pigeon	Mean responses in 10-s test periods to stimuli						
	Unmorphed dogs		Morphs			Unmorphed cats	
	Familiar	Novel	Mostly dog	Half dog	Mostly cat	Novel	Familiar
Group 60:40							
Cf	23.13	21.75	20.67	18.87	19.00	19.17	11.07
Ed	31.05	35.67	29.17	29.17	27.33	17.50	20.67
Ec	34.39	36.67	34.67	40.33	38.33	29.33	21.72
Sm	36.18	16.67	19.83	12.60	13.67	10.67	13.79
Sn	28.12	25.19	26.08	25.19	20.17	18.24	16.43
Group 80:20							
Ka	23.10	17.67	12.33	20.17	25.33	17.67	12.31
Ro	33.99	27.33	22.00	21.83	35.83	21.17	13.27
Ms	30.40	24.17	24.33	16.33	22.33	13.83	12.15
En	24.41	21.00	15.67	18.00	18.33	13.17	6.79
Da	9.04	8.83	7.83	8.33	5.67	3.33	2.26
Cu	26.32	25.17	21.00	16.17	24.50	26.17	17.40
Group 90:10							
Lo	20.21	11.17	17.83	9.33	11.17	7.50	1.79
Va	38.24	27.00	28.33	15.67	25.83	14.67	6.29
Cs	29.50	26.83	30.67	30.33	24.83	27.17	6.69
Dn	28.47	20.67	17.67	25.33	25.00	18.67	7.79
Pe	29.59	13.83	22.50	14.67	18.50	7.50	8.81
Zo	24.44	22.00	24.50	18.67	23.33	21.67	13.31

In the analysis of data from Test 1, when all stimulus types were entered into the analysis, the main effect of stimulus type and its interaction with group were both significant ($F_{4, 56} = 24.70$, $p < .001$, and $F_{8, 56} = 3.00$, $p < .01$, respectively); the main effect of group was not. A series of planned contrasts based on the full analysis were carried out to test the significance of the differences of means shown in Figure 5a. These tests revealed that, across the three groups, mean peck rates differed significantly between each stimulus type. Of these differences, that between the mostly dog and half dog stimuli was associated with the lowest F value ($F_{1, 14} = 8.11$, $p < .05$). None of these contrasts had significant interactions with groups.

To examine the origins of the interaction between groups and stimulus types, two further analyses were carried out. One used only the three stimulus types that were the same for all three groups (the training stimuli and the 50% morphs). The other used only the two stimulus types that differed for the two groups (the mostly dog and mostly cat stimuli); that is, the data shown in Figure 5b. In the common-stimulus analysis, only the main

effect of stimulus type was significant ($F_{2, 28} = 48.44$, $p < .001$). In the varying-stimulus analysis, both the main effect of stimulus type and its interaction with group were significant ($F_{1, 14} = 10.57$, $p < .01$, and $F_{2, 14} = 6.39$, $p < .05$, respectively).

Similar analyses were carried out for the second generalization test (see Figure 6). The main effect of stimulus type was significant ($F_{6, 84} = 27.16$, $p < .001$) but its interaction with group, and the main effect of group, were not. To ensure that this result was not due solely to the large difference between familiar and unfamiliar unmorphed exemplars that is obvious in Figure 6a, the analysis was repeated using only the five categories of transfer stimuli; similar results were obtained, and the main effect of stimulus type remained significant ($F_{4, 56} = 7.61$, $p < .001$). Planned contrasts were carried out to determine which of the differences that can be seen in the figures were significant. Contrasts based on the full analysis showed that (a) mean peck rates were significantly higher for familiar than for unfamiliar unmorphed dogs, and significantly lower for familiar than for unfamiliar cats; (b) that rates to the un-

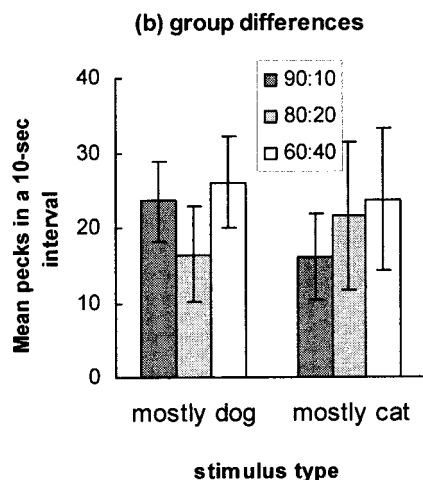
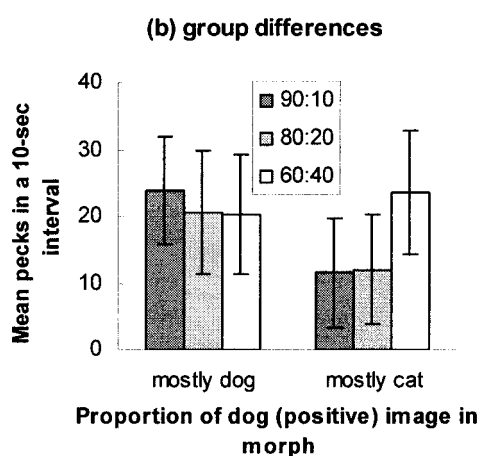
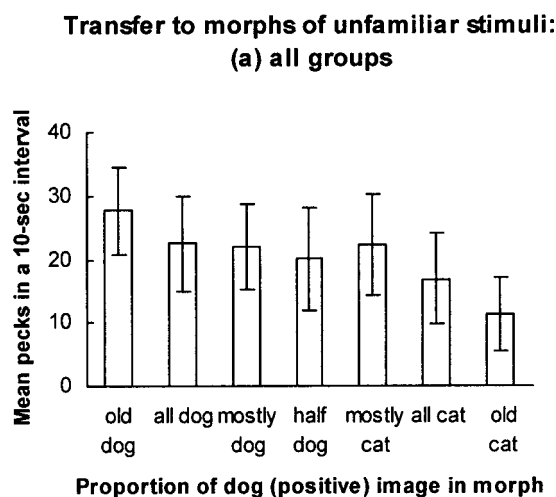
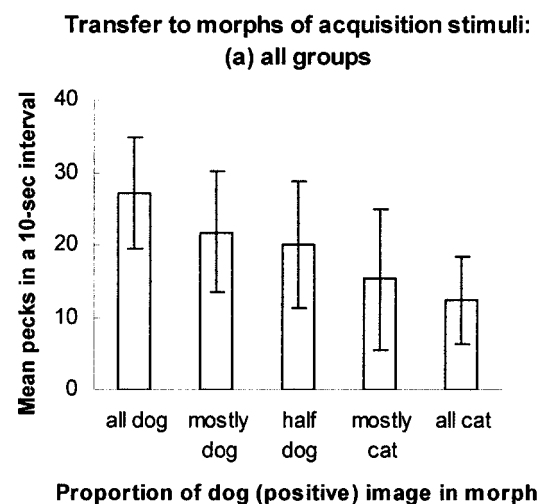


Fig. 5. Experiment 2: Results of generalization tests using morphs of training exemplars. In panel (a), the bars show mean response rates of all 17 pigeons to different types of stimuli during the 10-s nonreinforced period of test trials; stimulus types all dog and all cat were the stimuli used in training; the remainder were morphs. In panel (b) results for the mostly dog and mostly cat stimulus types are broken down by group, because for these stimulus types the images were different for the three groups. Error bars show standard deviations across pigeons.

Fig. 6. Experiment 2: Results of generalization tests using morphs of unfamiliar exemplars of the training categories. In Panel (a), the bars show mean response rates of all 17 pigeons to different types of stimuli during the 10-s nonreinforced period of test trials; data from training stimuli are included for comparison. In Panel (b) results for the mostly dog and mostly cat stimulus types are broken down by group, because the images for these stimulus types were different for the three groups. Error bars show standard deviations across pigeons.

morphed novel dogs were significantly higher than to the mostly dog morphs (though the difference is small), and significantly higher to the unmorphed novel dogs than to the mostly cat morphs; and (c) that peck rates to the 50% images were significantly lower than those to the mostly dog stimuli but did not

differ significantly from those to the mostly cat stimuli. Of these differences, that between the mostly dog and half dog stimuli was associated with the lowest F value ($F_{1,14} = 7.59$, $p < .05$).

Although the interaction between groups and stimulus types was not significant for the

Test 2 response rates, for comparability with the analysis of Test 1 rates, two further analyses of these data were carried out. As before, one used only the stimulus types that were the same for the three groups, and the other used only the stimuli that differed between them (i.e., the data plotted in Figure 6b). In the common-stimulus analysis, only the main effect of stimulus type was significant ($F_{2, 28} = 11.38, p < .001$). In the varying-stimulus analysis, no significant differences were found.

DISCUSSION

All the pigeons learned the category discrimination between images of dog heads and images of cat heads relatively quickly, and despite considerable decrement, showed clear generalization to new instances of the training categories (Figure 6). We can conclude that, like the whole dog and whole cat images of Experiment 1, the sets of images used in the present experiment formed perceptually coherent categories for the pigeons. As with the results of Experiment 1, however, there is no evidence as to whether the pigeons were able to relate the images to real dogs or cats, and it seems unlikely that they did so.

The rapid acquisition seen in the present experiment supports the conclusion drawn from Experiment 1 that the head regions of cats and dogs contain sufficient information for pigeons to form a concept discrimination between the two species, even if they are not the preferred source of information when body cues are also available. In the present experiment, the heads were shown at a larger scale than in Experiment 1, and without the potential distraction of the other parts of the body, so the present data are not inconsistent with the fact that pigeons did not necessarily use the head information when shown images of whole cats and dogs.

At the level of mean response rates, transfer to morphs of the training exemplars was very orderly, with both within-subject (Figure 5a) and between-subject (Figure 5b) comparisons showing that mean response rates fell systematically as the proportion of dog image in the morph declined (Figure 5). The only reversal from the monotonic trend was between the mostly-dog and mostly-cat images for the 60:40 group, and for these pigeons

the three kinds of morphed stimuli were closely similar. Although individual data (see Table 3) were inevitably less orderly, there is nothing in them to suggest that the smooth functions for the means were derived from step functions for individual pigeons. These results are comparable to those obtained by Makino and Jitsumori (2001, Figure 2) for test stimuli constructed by morphing between familiar positive and negative human face stimuli, although their procedure was not strictly comparable because their pigeons had learned a discrimination between particular faces that cut across the natural categorization by gender. Although there was some decrement even with the least amount of morphing, the data do not show a dramatic loss of discrimination for the mostly dog and mostly cat stimuli, suggesting that low spatial frequency information was able to support substantial generalization.

Transfer to morphs of novel exemplars was substantially less orderly. The pigeons clearly responded more to novel unmorphed dog head stimuli than to novel unmorphed cat head stimuli, and at intermediate rates to morphs formed from such stimuli (Figure 6a). Evidence of discrimination among the morphed stimuli was, however, weak; the planned contrasts found only one significant difference and the trends of the means shown in Figures 6a and 6b were not entirely systematic. Individual data (see Table 4) show considerable variety in trends. The lack of order in these data may well reflect compression of the data range due to generalization decrement: with new exemplars, the difference between the mean peck rates to 100% dog and 100% cat stimuli was only six pecks per trial, whereas the corresponding difference in the first generalization test, with training stimuli, was almost 15 pecks per trial. Peck rates to all morphed stimuli are expected to lie between these end points, and differences within such a small range are unlikely to emerge clearly within the limited number of trials that can be given in generalization tests.

These results are not consistent with the prediction that all morphed stimuli would lead to substantial generalization decrement because of the loss of high spatial frequency information. However, the substantial generalization decrement seen with unmorphed

novel exemplars (Figure 6a) does support the importance of high spatial frequencies, because the high spatial frequency information from the training stimuli is also lost when new exemplars are used.

GENERAL DISCUSSION

The present results add two more categories—whole dogs and cats, and dog and cat heads—to the long list of natural categories that birds have been trained to discriminate, with subsequent successful transfer to novel exemplars. It would have been surprising if a concept discrimination could not have been learned based on these images, but it is worth noting that the acquisition was relatively quick and that these categories are convenient for experimental use because exemplar images are readily available in large numbers and standard formats.

Chimeras and morphs are both ways of forming intermediates between stimuli, and they have in common that they involve varying many features at one time. They are therefore very different from the kind of transfer stimuli produced by systematic deletion of particular features. However, chimeras and morphs also differ sharply from each other. In general, chimeras preserve the high spatial frequency information that makes the recognition of detail possible, while destroying the lowest spatial frequency information that provides the image's overall shape; morphs attenuate both, but affect high spatial frequency information more immediately. The particular stimuli used in Experiment 1 were chosen with the intention that the chimeras would retain much of the low spatial frequency, overall shape information from one constituent (because to the human eye this information is largely represented in the body), and much of the high spatial frequency, detail information from the other constituent (because for humans this information is concentrated in the face area). Although the objective spatial frequency analysis of the stimuli showed that the roles of the two halves were, in fact, reversed, the intended dissociation was achieved, and the results support the suggestion that high spatial frequency information is particularly important in pigeons' pattern discrimination.

In both experiments, there was significant

generalization decrement from familiar to unfamiliar unmodified exemplars of the training categories. This is a further demonstration of the importance of absolute discrimination processes in pigeon concept discrimination. From the results of Experiment 1, it appears that absolute discrimination was applied to the body parts of the stimuli, and it was found, unexpectedly, that these were the richer in high spatial frequency information. Pigeons' dependence on local cues in pattern discrimination may therefore reflect a high memory capacity for this kind of cue in particular; this is consistent with the geon theory put forward by Wasserman *et al.* (1996).

From a comparative perspective, the results of Experiment 1 show marked differences from those found with human infants by Quinn and his colleagues (e.g., Spencer *et al.*, 1997). There was no evidence of a broadening of category content with increased exposure in pigeons; and pigeons' transfer behavior was dominated by body cues rather than head cues. This was despite the fact that the head cues were perceptually available, since they did exert some control over behavior (a conclusion that is reinforced by the results of Experiment 2, when the pigeons successfully discriminated heads).

Two conclusions can be drawn. First, these results make it more likely that the importance of head cues in human infants reflects the importance of the face in human social interaction rather than any general perceptual properties of the face stimulus. Human infants are disproportionately attentive to human faces from an early age, and it is likely that both dog and cat faces are sufficiently like human faces to draw attention. Second, the experiments provide further evidence that pigeons' discrimination is preferentially determined by local, high spatial frequency cues. More global, lower spatial frequency cues also play a part, as has been shown by Fremouw, Hebranson, and Shimp (1998) and Goto, Wills, and Lea (2004), and this is confirmed by the evidence of some control by head cues in Experiment 1, and by the smooth generalization to morphed stimuli in Experiment 2. It seems clear that the extent to which local-cue domination occurs will depend on the context, as Fremouw *et al.* (1998) and Cook (2001) have argued, and it

may even change dynamically (Fremouw, Herbranson, & Shimp, 2002). The present results suggest that an objective analysis of the high and low spatial frequency information actually available in stimuli might help clarify the circumstances under which local domination will be observed.

REFERENCES

- Aust, U., & Huber, L. (2002). Target-defining features in a "people-present/people-absent" discrimination task by pigeons. *Animal Learning & Behavior*, 30, 165–176.
- Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to visibility of gratings. *Journal of Physiology*, 197, 551–566.
- Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 3–16.
- Cerella, J. (1986). Pigeons and perceptrons. *Pattern Recognition*, 19, 431–438.
- Cook, R. G. (2001). Hierarchical stimulus processing. In R. G. Cook (Ed.), *Avian visual cognition*. Retrieved January 18, 2003, from <http://www.pigeon.psy.tufts.edu/avc>
- Cook, R. G., Wright, A. A., & Kendrick, D. F. (1990). Visual categorization in pigeons. In M. L. Commons, R. J. Herrnstein, S. M. Kosslyn & D. B. Mumford (Eds.), *Quantitative analyses of behavior: Vol. 8. Behavioral approaches to pattern recognition and concept formation* (pp. 187–214). Hillsdale, NJ: Erlbaum.
- Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical cells. *Journal of the Optical Society of America A: Optics Image Science and Vision*, 4, 2379–2394.
- Fremouw, T., Herbranson, W. T., & Shimp, C. P. (1998). Priming of attention to local or global levels of visual analysis. *Journal of Experimental Psychology: Animal Behavior Processes*, 24, 278–290.
- Fremouw, T., Herbranson, W. T., & Shimp, C. P. (2002). Dynamic shifts of pigeon local/global attention. *Animal Cognition*, 5, 233–243.
- Galton, F. (1883). *Inquiries into human faculty and its development*. London: Macmillan.
- Ghosh, N. (2002). *Discrimination of perceptually similar natural categories by pigeons*. Unpublished doctoral dissertation, University of Exeter.
- Goto, K., Wills, A. J., & Lea, S. E. G. (2004). Global-feature classification can be acquired more rapidly than local-feature classification in both humans and pigeons. *Animal Cognition*, 7, 109–113.
- Herrnstein, R. J., Loveland, D. H., & Cable, C. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 285–302.
- Huber, L., & Lenz, R. (1996). Categorisation of prototypical stimulus classes by pigeons. *Quarterly Journal of Experimental Psychology*, 49B, 111–133.
- Jitsumori, M., & Yoshihara, M. (1997). Categorical discrimination of human facial expressions by pigeons: A test of the linear feature model. *Quarterly Journal of Experimental Psychology*, 50B, 253–268.
- Lea, S. E. G. (1984). In what sense do pigeons learn concepts? In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp. 263–276). Hillsdale, NJ: Erlbaum.
- Lea, S. E. G., & Harrison, S. N. (1978). Discrimination of polymorphous stimulus sets by pigeons. *Quarterly Journal of Experimental Psychology*, 30, 521–537.
- Lea, S. E. G., Lohmann, A., & Ryan, C. M. E. (1993). Discrimination of 5-dimensional stimuli by pigeons: Limitations of feature analysis. *Quarterly Journal of Experimental Psychology*, 46B, 19–42.
- Makino, H., & Jitsumori, M. (2001). Category learning and prototype effect in pigeons: A study with morphed images of human faces. *Japanese Journal of Psychology*, 71, 477–485.
- Mareschal, D., French, R. M., & Quinn, P. C. (2000). A connectionist account of asymmetric category learning in early infancy. *Developmental Psychology*, 36, 635–645.
- Morgan, M. J., Fitch, M. D., Holman, M. D., & Lea, S. E. G. (1976). Pigeons learn the concept of an 'A'. *Perception*, 5, 57–66.
- Quinn, P. C., & Eimas, P. D. (1996). Perceptual cues that permit categorical differentiation of animal species by infants. *Journal of Experimental Child Psychology*, 63, 189–211.
- Quinn, P. C., Eimas, P. D., & Rosenkrantz, S. L. (1993). Evidence for representations of perceptually similar natural categories by 3-month-old and 4-month-old infants. *Perception*, 22, 463–475.
- Quinn, P. C., Eimas, P. D., & Tarr, M. J. (2001). Perceptual categorization of cat and dog silhouettes by 3- to 4-month-old infants. *Journal of Experimental Child Psychology*, 79, 78–94.
- Ryle, G. (1949). *The concept of mind*. London: Hutchinson.
- Spencer, J., Quinn, P. C., Johnson, M. H., and Karmiloff-Smith, A. (1997). Heads you win, tails you lose: Evidence for young infants categorising of mammals by head and facial attributes. *Early Development and Parenting*, 6, 113–126.
- Valenza, E., Simion, F., Cassia, V. M., & Umiltà, C. (1996). Face preference at birth. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 892–903.
- Vaughan, W., & Greene, S. L. (1984). Pigeon visual memory capacity. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 256–271.
- Wasserman, E. A., Gagliardi, J. L., Cook, B. R., Kirkpatrick-Steger, K., Astley, S. L., & Biederman, I. (1996). The pigeon's recognition of drawings of depth-rotated stimuli. *Journal of Experimental Psychology: Animal Behavior Processes*, 22, 205–221.

Received September 25, 2003

Final acceptance June 30, 2004